PALEOBOTANICAL EVIDENCE AND MOLECULAR DATA IN RECONSTRUCTING THE HISTORICAL PHYTOGEOGRAPHY OF RHIZOPHORACEAE[1]

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Abstract

The fossil record of the Rhizophoraceae includes numerous questionable identifications from strata of unconfirmed age, together with others representing clear evidence of the family in deposits whose age is well constrained by independent or multiple lines of evidence. *Bruguiera* or the *Bruguiera* lineage, and *Ceriops* are known from the early Eocene, *Kandelia* from the middle Eocene, and *Rhizophora* from the late Eocene. *Combretocarpus* is likely present by the middle Miocene, but it belongs to a family (Anisophylleaceae) earlier placed in the Rhizophoraceae that is now considered unrelated to that family. *Rhizophora*, as a genus, has existed essentially uninterruptedly in the Caribbean region since the late Eocene, but cooling events at ca. 15–14 Ma, ca. 3.4 Ma, and ca. 1.6 Ma, and the subsequent 18 to 20 glacial intervals provide a mechanism for development of the cold(er) tolerant populations toward the northern part of its range in the New World. In reconstructing the biogeographic history of *Rhizophora* in the Caribbean region, it is worthwhile noting that molecular-defined lineages (with little morphological or palynological variation) may have been introduced and gone extinct on multiple occasions. This allows for variation in molecular patterns and apparent stasis in the fossil record—a possibility not widely considered in the literature. The most recent molecular-defined common ancestor to existing populations is estimated to have arrived in the New World ca. 11 Ma, using an origin in the Paleocene (ca. 60 Ma) as the basis for calculation.

Key words: fossils, historical phytogeography, Rhizophoraceae.

Resumen

El registro fósil de Rhizophoraceae incluye numerosas identificaciones cuestionables de estratos sin edad confirmada, junto con otros que representan clara evidencia de que la familia se encuentra en depósitos cuya edad está forzada por líneas de evidencias independientes o múltiples. *Bruguiera* o el linaje *Bruguiera*, y *Ceriops* se conocen del Eoceno temprano, *Kandelia* del Eoceno medio y *Rhizophora* del Eoceno tardío. *Combretocarpus* está presente probablemente a partir del Mioceno medio, pero pertenece a una familia (Anisophylleaceae) ubicada anteriormente en Rhizophoraceae que ahora se considera sin relación a esa familia. *Rhizophora*, como género, ha existido esencialmente sin interrupción en la región del Caribe desde el Eoceno tardío, pero eventos de enfriamiento hace ca. 15–14 Ma, ca. 3.4 Ma y ca. 1.6 Ma, y los subsecuentes 18 a 20 intervalos glaciales proporcionan un mecanismo para el desarrollo de poblaciones tolerantes al frío hacia la parte norte de su distribución en el Nuevo Mundo. Al reconstruir la historia biogeográfica de *Rhizophora* en la región del Caribe, cabe observar que linajes moleculares (con poca variación morfológica o palinológica) pudieron haber aparecido y extinguido en múltiples ocasiones. Esto permite la variación en patrones moleculares y aparente estasis en el registro fósil – una posibilidad no ampliamente considerada en la literatura. El antepasado común de definición molecular más reciente de las poblaciones existentes se estima que llegó al Nuevo Mundo hace ca. 11 Ma, si se usa un origen en el Paleoceno (ca. 60 Ma) como la base para el cálculo.

Investigations of fossil *Rhizophora* L. in the Caribbean, in association with studies on phylogeny (Schwarzbach & Ricklefs, 2000), have led to this review of reports of the family Rhizophoraceae worldwide. One purpose of the review is to discern from the numerous reports of Rhizophoraceae, from strata purportedly ranging in age from the Cretaceous to the Recent, identifications and ages that afford a reliable basis for reconstructing the evolution and historical biogeography of the family. From that base, the gradual accumulation of new evidence from genes, molecules, morphology, and fossils will allow continuing revision in concepts, and the increasing integration of the historical record with biogeographic and phylogenetic patterns derived from modern systematic approaches.

Modern Distribution and Global Fossil Records of Rhizophoraceae

The circumscription of extant Rhizophoraceae and Anisophylleaceae (included within the Rhizophoraceae by some authors; e.g., Melchior, 1964) is listed in

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[1] Information on molecular systematics was provided by Andrea Schwarzbach from on-going studies by her and collaborators on the Rhizophoraceae, and on the fossil records by Aaron M. Ellison, Jeri Kvacek, M. K. Macphail, and Peter Saenger. The manuscript was read by Robyn J. Burnham, Aaron M. Ellison, Shirley A. Graham, and Andrea Schwarzbach.

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Table 1. Circumscription of Rhizophoraceae and Anisophyllaceae by various authors as given in Schwarzbach and Ricklefs (2000). * indicates genera reported in the fossil record.

Rhizophoraceae		
	Macarisieae	
		Anopyxis Pierre ex Engl.
		Blepharistemma Wall. ex Benth.
		Cassipourea Aubl.
		Comiphyton Floret
		Dactylopetalum Benth.
		Macarisia Thou.
		Sterigmapetalum Kuhlm.
	Gynotrocheae	
		Carallia Roxb.
		Crossostylis J. R. Forst. & G. Forst.
		Gynotroches Blume
		Pellacalyx Korth.
	Rhizophoreae	
		**Bruguiera* Lam.
		**Ceriops* Arn.
		**Kandelia* (DC.) Wight & Arn.
		**Rhizophora* L.
	Anisophylleaceae	
		Anisophyllea R. Br.
		**Combretocarpus* Hook. f.
		Poga Pierre
		Polygonanthus Ducke

Table 1. It is noted that the Anisophylleaceae is recognized as a separate and unrelated family by Schwarzbach & Ricklefs (2000), and of the 15 genera included in the Rhizophoraceae, only four (tribe *Rhizophoreae*) are exclusively mangroves.

Only five of these genera have been reported in the fossil record. For some, the age of the strata has not been firmly established, the identifications have not been confirmed or have been questioned, and broad or tentative identifications by the original author(s) have achieved greater certainty with repetition in the later literature. For purposes of biogeography, paleoenvironmental reconstructions, tracing lineages, and calibrating molecular data for taxa in which there is a relatively extensive fossil record, it is useful to have one set of paleobotanical evidence limited to reports in which the taxonomic level of the identifications is unambiguous, the age of the strata is well established, and the implications of the record are conservatively interpreted. For the Rhizophoraceae this record begins in the early Eocene (ca. 50 Ma; million years, millions of years ago), and for *Rhizophora* it begins in the middle to late Eocene (ca. 45 Ma; Table 2). The incorporation of more tentative data allows development of further theories and models of interest provided the assumptions, speculations, and acceptance of provisional identifications are clearly designated. This more inclusive record for the Rhizophoraceae and *Rhizophora* extends the range into the Paleocene (ca. 60 Ma; e.g., Gruas-Cavagnetto, 1976; Thanikaimoni, 1987). Where both kinds of evidence are part of the overall record, it is worthwhile to have two calculations that bracket the potential evolutionary history of the lineage.

Pollen of the *Combretocarpus*-type (Anisophyllaceae; Muller, 1981) was recovered from late Miocene deposits in northwestern Borneo (Anderson & Muller, 1975). A single grain was found in the Miocene Berakas coal, and the pollen became frequent in the Holocene Marudi peat. Morley (1977) found it in the middle Miocene of the same area. Thus, if the family has a fossil record, and this has not been established, it consists of pollen of the *Combretocarpus*-type, possibly representing the Anisophylleaceae, from the middle Miocene to Holocene of Borneo. If the pollen is *Combretocarpus*, and knowing that the original author (Muller, 1964) did not report it from other material studied from Borneo, the Maracaibo region of northern South America, or from extensive projects by Bataafse Internationale Petroleum Maatschappij (Shell Oil Company) in Nigeria and elsewhere (Germeraad et al., 1968), it is reasonable to assume that the middle Miocene marks the early appearance of *Combretocarpus* of the Anisophylleaceae. This is younger than the minimum age for the Rhizophoraceae (see below), and it will be interesting to see if this temporal sequence of the two families, and its phylogenetic implication, remain true with further phylogenetic and paleobotanical study.

In the Rhizophoraceae, fruits of *Kandelia* Wight & Arn. are reported from the middle Eocene of Alaska (Wolfe, 1972, 1977). A hypocotyl of † (= fossil) *Ceriops cantiensis* is reported from the London Clay flora of England (early Eocene, Ypresian; 52–49 Ma (Collinson, 1983)), and pollen is reported from the late Miocene of the Marshall Islands (Leopold 1969; listed as pending in Muller, 1981) and possibly from the late Eocene of southwestern Australia (Churchill, 1973). The latter is not a definite report of *Ceriops*, but the author regarded it as possibly present among the abundant and morphologically similar *Rhizophora* pollen. Hypocotyls resembling *Bruguiera* are known from the London Clay and are identified as †*Palaeobruguiera* (Collinson, 1983). Starch grain casts and molds similar to those of modern *Ceriops* and *Bruguiera* have also been found in the London Clay (Wilkinson, 1983). Reports of fossils with uncertain generic identifications include pollen similar to *Rhizophora* or *Kandelia* from the earliest Eocene of France (Gruas-Cavagnetto et al., 1988) and *Bruguiera*-type pollen of the same age in the Paris Basin

Table 2. Reports of *Rhizophora* in the fossil record of the Caribbean region. Fm(s)=formation(s). BP = before present.

Age/formation	Locality	References
Eocene/El Bosque, La Trinidad Fms	Chiapas, Mexico	Tomasini-Ortiz & Martínez-Hernández, 1984
Middle to Late Eocene/Gatuncillo Fm	Panama	Graham, 1985
Late Eocene to Present	Maracaibo Basin, Venezuela	Germeraad et al., 1968; Lorente, 1986
Oligocene	Colombia	Lorente, 1986
Middle Oligocene/San Sebastian Fm	Puerto Rico	Graham & Jarzen, 1969
Middle Oligocene/San Sebastian Fm	Puerto Rico	Hollick, 1928
Oligocene to Present	Brazil	Lorente, 1986
Oligocene to Miocene	Colombia	Lorente, 1986
Early Miocene/Culebra, Cucaracha, La Boca Fms	Panama	Graham, 1988a, b, 1989
Early Miocene/La Quinta Fm	Chiapas, Mexico	Langenheim et al., 1967; Graham, 1999c
Early Miocene/Ixtapa Fm	Chiapas, Mexico	Martínez-Hernández, 1992
Early to Middle Miocene	Venezuela	Lorente, 1986
Early to Middle Miocene	Venezuela	Berry, 1922
Early to Late Miocene	Brazil/Colombia	Hoorn, 1994a, b, c
Late Miocene/Gatun Fm	Panama	Graham, 1991a, b
Pliocene/Herrería Fm	Guatemala	Graham, 1998
Middle Pliocene/Paraje Solo Fm	Veracruz, Mexico	Graham, 1976
Middle Pliocene/Uscari Fm (age fide Collins to Burnham, pers. comm.)	Costa Rica	Graham, 1987
Quaternary		
Late glacial-Holocene	Yucatan Peninsula	Leyden et al., 1994
Holocene	Middle American Trench, Tehuantepec, Mexico	Habib et al., 1970
Holocene	Isla Juventud, Cuba	Moncada Ferrera et al., 1990–1991
35,000 yrs BP	Gatun Lake, Panama	Bartlett & Barghoorn, 1973
12,000 yrs BP	Gatun Lake, Panama	Bartlett & Barghoorn, 1973
7000 yrs BP	Playa Medina, NE Venezuela	Vegas & Rull (in ms.)
5100 yrs BP	Bragança Peninsula Pará, Brazil	Behling et al., 2001
Holocene	Trinidad	Berry, 1925
Holocene	Brazil [Other reports of Rhizophoraceae/*Rhizophora* from Latin America][1]	Behling, 1996
Paleocene/Cerro Boraró Fm	Chubut, Argentina	Petriella, 1972[2]
Late Eocene to Early Oligocene/Potoco Fm	Altiplano, Bolivia	Horton et al., 2001[3]

[1] Various reports of pollen from the Paleocene to Eocene of northern South America by van der Hammen & Wijmstra (1964) and Wijmstra (1971) are now assigned by the authors to the late Eocene or younger. Another South American record is †*Zonocostites ramonae* (pollen) from various sites on the continental platform off eastern Brazil, Late Cretaceous to Oligo-Miocene, in a technical report by Pares Regali et al. (1974a).

[2] Tentative reference of generalized wood to Rhizophoraceae.

[3] †*Zonocostites ramonae*, biological affinities are not cited by the author.

and in southern France (Gruas-Cavagnetto, 1991; Gruas-Cavagnetto et al., 1980). Pollen of *Bruguiera*-type (see *B. gymnorhiza*) is reported from the late Miocene of the Marshall Islands (Leopold, 1969; considered pending by Muller, 1981), and from the Oligocene of England (*Bruguiera parviflora* (Roxb.) Wight & Arn.-type; Machin-Pallot, 1971). With regards to the latter, Muller (1981: 63) notes that "Careful comparison failed to confirm this identification. Points of difference are the more prolate shape, less pronounced costae along the colpi, the indistinct endoaperture and thin, psilate exine." Among members of the Rhizophoraceae, those with the most convincing fossil record are *Kandelia* from the late middle Eocene of Alaska (Wolfe, 1972, 1977), and *Ceriops* and *Bruguiera* both from the early Eocene of England (Collinson, 1983; Wilkinson, 1983) and the Miocene of the Marshall Islands (Leopold, 1969).

The earliest fossil record of *Rhizophora* is difficult to establish because of the uncertainty of some identifications and the unsettled age of some strata. Several geologic range charts have been published that include *Rhizophora* (Germeraad et al., 1968; Rico-Gray, 1993; Saenger, 1998; Ellison et al., 1999;

Morley, 2000), and summaries are available of the global record (Muller, 1981; Plazait et al., 2001) and of more specific areas: Mexico (Langenheim et al., 1967), the Caribbean Basin region (Graham, 1995), Maracaibo Basin (Rull, 1998), the southeastern Pacific (Hekel, 1972; Churchill, 1973; Anderson & Muller, 1975; Mepham, 1983; Ellison, 1991), and India (Prakash, 1960; Thanikaimoni, 1987).

Muller (1981: 62) was of the opinion that, "The oldest records [of *Rhizophora*] are still the upper Eocene occurrences of *Zonocostites ramonae* Germeraad, Hopping & Muller reported by Germeraad, Hopping, and Muller (1968) from the Caribbean area and confirmed by Pares Regali, Uesugui, and Santos (1974a, b) in Brazil." Several older records were rejected by Muller: the middle Eocene of India (Venkatachala & Rawat, 1972, 1973), because the basis for the age assignment is unclear, "and since the subzone is the uppermost one, an upper Eocene age appears possible" (Muller, 1981: 63); the Paleocene and lower Eocene of western Europe (Gruas-Cavagnetto, 1976; Krutzsch, 1969, 1970; Krutzsch & Vanhoorne, 1977), because the authors allied †*Tricolporopollenites mansfeldensis* with *Rhizophora* on the basis of similarities in morphology that were questioned; and the Cretaceous (Maestrichtian) of Canada (*Rhizophora*-type; Jarzen, 1978), because the fossils are characterized by much wider endoapertures, lack of polar costae, lack of colpi, and have a uniform granular structure. A record in the Ilerdien or Ypresian (earliest Eocene) of "Rhizophoraceae?" from the Pyrenees region (Gruas-Cavagnetto et al., 1988: 221) is uncertain because distinct colpi transversalis are not evident in the photograph; it should be noted that the specimens are identified in the text as "Rhizophoraceae?" while on the range chart the question mark does not appear (Gruas-Cavagnetto et al., 1988: 221 and 222, respectively). In the IOP (International Organization of Palaeobotany) Plant Fossil Record Data Base (www.biodiversity.org.uk), the Ilerdien/Ypresian record is listed under Rhizophoraceae as ?first occurrence.

There are reports of Rhizophoraceae in even older deposits in the early literature, but none of these have been confirmed: †*Rhizophorites bombacaceus* Bayer (leaf, affinites cited as with Rhizophoraceae) from the Cenomanian (early late Cretaceous) of Bohemia (Bayer, 1914) and †*Rhizophorocarpus dekapetalus* Velenovský & Viniklář (fruit, Rhizophoraceae) from the Cretaceous of Bohemia (Velenovský & Viniklář, 1926) as listed in the Andrews (1970) catalog. No pre-late Eocene records for the family or the genus *Rhizophora* are listed in the LaMotte (1952) catalog. The Bohemia fossils would be older by 50 Ma or more than any confirmed Rhizophoraceae. The specimen of *R. dekapetalus* is in the National Museum in Prague (J. Kvacek, pers. comm.); the location of *R. bombacaceus* is unknown. Neither genus is regarded as belonging to the Rhizophoraceae by Kvacek, who is working on the Bohemian Cretaceous floras, and he notes (pers. comm.) that in almost every case the generic determinations by Bayer and particularly Velenovský are proving incorrect.

The same concerns raised by Muller (1981) about the original identifications, subsequent confirmation or acceptance of the identifications, and/or age of the strata also apply to other pre-late Eocene reports listed in the range charts previously mentioned. These include *Rhizophora* from the Paleocene (Thanikaimoni, 1987) and early Eocene (Prakash, 1960; Lakhanpal, 1970) of India. The author's efforts to communicate about the status of the India specimens were not successful.

Rhizophora was reported from Borneo in beds initially assigned to the middle Eocene (Muller, 1964), but the age was later emended to the late Eocene by Muller (1981). In the Australasian region in general, and in Australia in particular where the Cenozoic plant microfossil record is extensive, "the earliest Rhizophoraceae (*Zonocolpites ramonae*) are middle late Eocene from the offshore Browse Basin in NW Australia" (MacPhail, pers. comm.; MacPhail, 1999). This is in contrast to older records (late Paleocene (60 Ma), and early Eocene (50 Ma)) from Australia and India cited in the summary by Saenger (pers. comm.; Saenger, 1998).

Considering the critical importance of the earliest records of a lineage in deciphering its phylogeny and biogeography, a conservative reading of the evidence is warranted. *Rhizophora*, as a modern genus reflected by the morphology of its pollen and its mangrove habitat, is first known in the late Eocene and appears almost simultaneously in the Old and New World tropics. This implies an earlier origin for the genus, possibly in the southeast Asia–eastern Tethys Sea region (Raven & Axelrod, 1974; Ellison, 1991), and the change from its absence in the middle Eocene to its dominance in many tropical coastal habitats in the late Eocene suggests rapid migration, and an origin in, or a rapid adjustment to, its present specialized habitat.

Among genera of Rhizophoraceae, *Rhizophora* appears somewhat later (late Eocene) than *Kandelia* (late middle Eocene) and *Ceriops/Bruguiera* (early Eocene), according to the data presented. However, the sequences of appearance are geologically close in time, and additional paleobotanical information and phylogenetic studies are needed to establish the time, place of origin, diversification, and radiation of the family.

THE CARIBBEAN FOSSIL RECORD OF *RHIZOPHORA* (TABLE 2)

Confidence that advancement has been made in understanding complex biological systems is enhanced when results from two independent lines of inquiry are congruent. Opportunity for achieving a new paradigm is presented when incongruous or partially incongruous data sets are reconciled, or when one data set limits the choices or supports a single interpretation from among several generated by another approach. Investigations into the historical biogeography of *Rhizophora* in the Caribbean region through paleobotanical techniques and by molecular approaches provide such an opportunity for discovering consistencies in interpretation, identifying apparent inconsistencies, and formulating hypotheses to explain the differences. There is clearly much left to do, as is evident, for example, from the view expressed by Ellison et al. (1999: 95) that "... regional species diversity [of mangroves] resulted from *in situ* diversification after continental drift" and by Plaziat et al. (2001: 1961) that "It is therefore clear that continental drift had a limited role in the dispersal and development of modern mangrove floras." The Caribbean region is a suitable place for comparing the fossil record with speciation models derived from molecular systematics, because the history of *Rhizophora* there is one of the best documented in the world.

A scenario for the origin and spread of the mangrove lineage (4 of 15 genera) within the Rhizophoraceae, based on interpretation of presently available molecular data, and augmented by information from the fossil record, is presented by Schwarzbach & Ricklefs (2000, 2001). The essentials of that scenario, as it relates to the Caribbean Basin, are as follows:

(1) *Rhizophora* reached the New World about 40 Ma (based on evidence from the fossil record).
(2) The genus underwent range contraction and extinction in the late Tertiary associated with cooling climates (evidence for cooling climates is based on the fossil record and other geological evidence).
(3) The genus may have disappeared from the Atlantic and Caribbean regions (a possible interpretation of the molecular data).
(4) If so, *Rhizophora* was probably re-introduced about 11 Ma (a possible interpretation of the molecular data using a date of 60 Ma for the origin of the family).

To better constrain the time during which *Rhizophora* most likely would have disappeared from the Caribbean region ("the late Tertiary, probably associated with cooling climates" (Graham, 1999a: 87)), the following summary is presented of the relevant global paleoclimatic trends as a context for assessing the Caribbean record. Beginning with the end of the hot house interval near the early Eocene/middle Eocene boundary (ca. 52 Ma):

Early Eocene—earliest mountain glaciers first appeared on Antarctica (Birkenmajer, 1990).
Late middle Eocene and early Oligocene—limited ice sheets appeared along the margin of Antarctica (Leg 119 Shipboard Scientific Party, 1988).
Early/late Oligocene boundary (ca. 30 Ma)—more extensive ice developed on Antarctica (Miller et al., 1987; Poore & Matthews, 1984), as reflected in a major drop in global mean sea level (see Graham, 1999a: 95).
Middle Miocene (15–14 Ma)—permanent ice formed on Antarctica and glacial climates developed in the Arctic.
Middle Pliocene (ca. 3.4 Ma)—extensive northern hemisphere glaciation began (Shackleton & Opdyke, 1977).
Quaternary (ca. 1.6 Ma)—ice age began; present interglacial began ca. 11 Kyr (thousand years, thousands of years ago).

If cooling climate was a factor in the possible disappearance of *Rhizophora* from the Caribbean region in the late Tertiary, 15–14 Ma would be a likely time as shown by the initiation of permanent ice on Antarctica, glacial climates in the Arctic region, and a number of terrestrial vegetational responses on a global scale (e.g., the trend toward replacement of forest by grasslands in mid-continent North America (Graham, 1999a) and the disappearance of warm elements from the flora of New Zealand (Lee, pers. comm.)). Beginning about this time, changes also occurred in the vegetation of northern Latin America that would be consistent with, and reciprocal to, a restriction in the range of *Rhizophora* due to cooling climates. The principal change was the introduction of an increasing number of northern temperate elements progressively farther south into the lower latitudes (*Abies* Mill., *Picea* A. Dietr., *Pinus* L., *Alnus* L., *Celtis* L., *Fagus* L., *Juglans* L., *Liquidambar* L., *Myrica* L., *Populus* L., *Ulmus* L.; Graham, 1999b). These events identify the most likely beginning for any disappearance of *Rhizophora* from the Caribbean region at 14–15 Ma. The 3–4 Ma period between 14–15 Ma and *Rhizophora*'s estimated return at ca. 11 Ma corresponds to the Serravallian Stage of the middle Miocene (10.4–14.2 Ma; Harland et al., 1989), and is part of the 'ice house' interval when global climates were becoming cooler. In the combined analyses by Schwarzbach & Ricklefs (2000, 2001; Schwarzbach, pers. comm.), a maximum age of 60 Ma is used for the earliest *Rhizophora* from which a New World/Old World split in *Rhizophora*, and its reintroduction into the New World at 11 Ma is calculated. When the younger age of ca. 45 Ma is used (Schwarzbach, in prep., pers. comm.), bracketing the possibilities afforded by the fossil record, that split and any reintroduction into the New World has a younger dating. Thus, the initial appearance of

Rhizophora in the Caribbean and its subsequent record is of interest.

Beginning in the Quaternary, it is probable that the range of *Rhizophora* in the Caribbean region fluctuated with changes in temperature, salinity, and sea level (see Blasco et al., 1996). However, if *Rhizophora* disappeared as a consequence of the colder-than-at-present intervals of the past 2 Ma, then accommodation must be made for the likelihood of 18 to 20 of these presence/absence cycles, because that is the number of such cold intervals documented for the Quaternary Period in the northern latitudes (Milankovitch eccentricity cycles of 100 Kyr; see papers cited in Graham, 1999a: 37–41); the effect of these cold intervals on biotas is now known to have extended into the low latitudes, as shown by strontium/calcium ratio data from Barbados corals (Guilderson et al., 1994) and North Atlantic Heinrich events reflected in pollen sequences from south-central Florida (Grimm et al., 1993; see papers cited in Graham, 1999a: 283). There are no plant fossil-bearing sections that extend back into one or more of the glacial maxima in the Caribbean region to provide direct evidence of its history during the cold periods (e.g., at 18 Kyr). However, the paleobotanical evidence that is available suggests that *Rhizophora* did not disappear and return 18 to 20 times during the past 2 Ma in that region (Table 2). For example, sediment cores from Gatun Lake, Panama show that at ca. 35 Kyr *Rhizophora* pollen comprised 74% of the total palynomorph assemblage, and it has been present in varying amounts for the past 12 Kyr (Bartlett & Barghoorn, 1973). At any rate, brief, relatively recent, rapid, and partial range restrictions are not the kind needed to explain that aspect of the molecular data open to the possible interpretation of a 3–4 Ma absence from the Caribbean region between 15–14 to 11 Ma. The cooling events at 15–14 Ma, 3.4 Ma, 1.6 Ma, and the fast-paced glacial-interglacial fluctuations of the Quaternary Period do, however, provide a mechanism for the presence of cold(er) tolerant populations of *Rhizophora* in southern Florida, Jamaica, St. Croix, and Texas mentioned by Schwarzbach & Ricklefs (2001).

For the Tertiary, the question is whether it is a viable option, in interpreting the molecular data, to assume that *Rhizophora* was absent from the Caribbean region for a significant span of time after its initial appearance in the late Eocene. The Caribbean fossil record of *Rhizophora* is based on fossil pollen, known in the stratigraphic literature as *Zonocostites ramonae*. Numerous well cores have been drilled and examined extensively for plant microfossils in the petroleum-rich Caribbean Basin; *Rhizophora* pollen is distinctive and easily recognizable at the generic level (Langenheim et al., 1967; Muller & Caratini, 1977) and is an indicator of depositional environments—an important aspect of petroleum geology. For these reasons, the stratigraphic range of *Rhizophora* pollen in the Caribbean Basin is well known and can be confidently fixed as beginning in the late Eocene. The oldest occurrences are in the late Eocene Gatuncillo Formation of Panama, and the early to middle part of the late Eocene of Venezuela (Maracaibo Basin; Germeraad et al., 1968; Lorente, 1986), corresponding to a time period around 45–40 Ma.

Regarding the subsequent history of *Rhizophora*, Lorente (1986) studied a section from the late Tertiary of Venezuela that includes the interval from the early to middle Miocene (Burdigalian to Langhian), and *Zonocostites ramonae* is present throughout. It has also been reported from the Oligocene to Miocene of Colombia, from the Oligocene to the Recent of Brazil, and from the late Eocene to the Recent generally throughout northern South America (Germeraad et al., 1968; Lorente, 1986); in early (Graham, 1988a, b, 1989) and late (Graham, 1991a, b) Miocene deposits in Panama; and in Pliocene sediments from Mexico (Graham, 1976). In both published and unpublished studies, *Rhizophora* is almost universally present from the late Eocene to the Recent in pollen/spore-bearing sediments from coastal habitats throughout the Caribbean Basin, and there is no evidence for a 3–4 Ma gap between 15–14 and 11 Ma, or at any time in the post late Eocene record.

A second point based on paleontological evidence concerns a cause for a possible disappearance of *Rhizophora*, and the timing of its subsequent return. If cooling temperatures were a reason for its disappearance at 15–14 Ma, it must be noted that the global paleotemperature curve shows that it was even colder at 11 Ma (Graham, 1999a: 89). This makes it difficult to explain its re-introduction under conditions more severe than those purported to explain its disappearance. There are no abrupt, short-lived, extensive catastrophic events known for the Tertiary interval involved, and fossil records from other groups do not show a response to such an event. Habitat reduction is unlikely during the time under consideration, because coastal environments were expanding with the fall in sea levels as glaciers began to develop more extensively.

It is clear that phylogenetic information alone does not discriminate among all possible patterns, and information from the fossil record can help to limit the different options. Also, the fossil record can help discriminate between a continuous presence and periodic absences as a result of catastrophic events. In the case of a continuous presence there should be a relatively uninterrupted fossil record, while catastrophic events should produce gaps in that record, likely accompained by similar evidence from adjacent regions, and this evidence is not present.

However, there are several limitations that must be acknowledged in reconstructing the historical biogeography of *Rhizophora* based on evidence from fossil pollen. Its history (Graham, 1995) is derived from records that for any one region may be intermittent for several reasons. One is that many samples are derived from roadside, streamside, and surface mine exposures that are widely separated both geographically and stratigraphically. Another is that even in cores resulting from drilling operations, there are zones missing or barren of terrestrial plant microfossils because there are changes in depositional environments (e.g., inundation, marine regression and erosion), the complete section was not studied, or selected results were considered proprietary and unpublished. A third reason is that tropical pollen and spore-bearing lignites, clays, and siltstones may be lain down under different depositional environments. Those deposited at the coastal interface between terrestrial and marine habitats frequently contain *Rhizophora* pollen (e.g., the middle Pliocene Paraje Solo Formation of Mexico; the early Miocene Culebra, Cucaracha, and La Boca formations of Panama; the late Miocene (fide Collins, pers. comm. to Burnham) Gatun Formation of Panama; Table 2). Similar sediments, but deposited in inland swamps, or upland bogs and marshes, removed from the influence of marine waters, do not contain *Rhizophora* pollen (e.g., the late Miocene Padre Miguel Group of Guatemala). For these reasons, range charts with continuous lines (e.g., Germeraad et al., 1968, fig. 15) imply the continual presence of a taxon over millions of years, but this can be misleading because sections for the Tertiary are not sufficiently continuous to detect absences of several thousands or tens of thousands of years. For *Rhizophora*, however, the combined records reduce the possibility of an absence even for this duration.

Another limitation to the paleopalynological approach for the present study is the taxonomic level to which *Rhizophora* pollen can be recognized. It is important to note that lineages here refer to molecular-defined lineages; in terms of morphology, including pollen morphology, the genus is not readily subdivided into clearly recognizable taxa. Langenheim et al. (1967) and others have studied the morphology of *Rhizophora* pollen, and based on the complete geographic and morphologic range of the genus they have concluded that no ecological or taxonomic categories can be consistently recognized on the basis of pollen characters. This leaves open the possibility that different lineages, defined by molecular and/or non-pollen morphological characters, may have migrated in and out of the region, leaving no evidence of the fluctuations in the plant microfossil record. This possibility has not been widely emphasized in the literature tracing the geologic record of lineages, but it will be increasingly important as histories based on paleobotanical evidence are integrated with those derived from molecular studies. In the case of *Rhizophora*, the stenopalynous condition of the pollen allows for the possibility of repeated introductions and extinctions of molecular- and otherwise-defined lineages. However, the coarse resolution of the fossil record, sea-level and paleotemperatures trending in the wrong direction, and undetected or selective catastrophies cannot be invoked to support a prolonged absence of *Rhizophora*, as a genus, from the Caribbean region after the late Eocene.

According to the fossil record, *Rhizophora* has been widespread in the New World since its initial appearance in about the late Eocene. No major gaps are apparent in its distribution since that time, and there is no evidence for region-wide catastrophic events. The model around which consensus is developing is one that involves frequent extinction and reintroduction of molecular-defined lineages, and pollen that documents the presence of *Rhizophora*, as a genus, in the Caribbean region since the late Eocene. According to recent calibration data (Schwarzbach & Ricklefs, unpublished data) the most recent common ancestor or colonizer that spread throughout the New World arrived about 11 Ma and diversified in response to environmental change. Consistent with the model are the documented climatic fluctuations and changes in the physical environment (Graham, 2003a, b, c) now known to have affected the Caribbean region and the associated changes in sea level and ocean salinity concentrations resulting from rapid glacial and interglacial transitions. Results from molecular-based studies may assume (1) intuitively a Paleocene origin (ca. 60 Ma) for the family because of its distribution and diversity in the Eocene, and (2) an Eocene origin (ca. 45 Ma) based on a conservative reading of the existing fossil record. These bracket the plausible options, and define critical time intervals where additional, verifiable records should be sought.

Literature Cited

Anderson, J. A. R. & J. Muller. 1975. Palynological study of a Holocene peat and a Miocene coal deposit from NW. Borneo. Rev. Paleobot. Palynol. 19: 291–351.

Andrews, H. N. Jr. 1970. Index of generic names of fossil plants, 1820–1965. Bull. U.S. Geol. Surv. 1300: 1–354.

Bartlett, A. S. & E. S. Barghoorn. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). Pp. 203–299 *in* A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Science Publishers, Amsterdam.

Bayer, E. 1914. Fytopalaeontologicke příspěvky ku Poznání českých křidových vrstev peruckých. Arch. Přír. Výzk. Čech 25: 1–66.

Behling, H. 1996. First report on new evidence for the occurrence of *Podocarpus* and possible human presence at the mouth of the Amazon during the Late-glacial. Veg. Hist. & Archaeobot. 5: 241–246.

———, M. C. L. Cohen & R. J. Lara. 2001. Studies on Holocene mangrove ecosystem dynamics of the Bragança Peninsula in north-eastern Pará, Brazil. Palaeogeogr. Palaeoclimatol. Palaeoecol. 167: 225–242.

Berry, E. W. 1922. Tertiary fossil plants from Venezuela. Proc. U. S. Natl. Mus. 59: 553–579.

———. 1925. A Pleistocene flora from the island of Trinidad. Proc. U. S. Natl. Mus. 66: 1–9.

Birkenmajer, J. 1990. Geochronology and climatostratigraphy of Tertiary glacial and interglacial succession on King George Island, South Shetland Islands (West Antarctica). Pp. 111–151 *in* H. Miller, Zentralblatt für Geologie und Paläontologie Teil I, Workshop on Antarctic geochronology. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.

Blasco, F., P. Saenger & E. Janodet. 1996. Mangroves as indicators of coastal change. Catena 27: 167–178.

Churchill, D. M. 1973. The ecological significance of tropical mangroves in the early Tertiary floras of southern Australia. Geol. Soc. Australia Special Pap. No. 4: 79–86.

Collinson, M. E. 1983. Fossil plants of the London Clay. Field Guides to Fossils No. 1. The Paleontological Association, London.

Ellison, A. M., E. J. Farnsworth & R. E. Merkt. 1999. Origins of mangrove ecosystems and the mangrove biodiversity anomaly. Global Ecol. Biogeogr. 8: 95–115.

Ellison, J. C. 1991. The Pacific palaeogeography of *Rhizophora mangle* L. (Rhizophoraceae). Bot. J. Linn. Soc. 105: 271–284.

Germeraad, J. H., C. A. Hopping & J. Muller. 1968. Palynology of Tertiary sediments from tropical areas. Rev. Paleobot. Palynol. 6: 189 348.

Graham, A. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787–842.

———. 1985. Studies in neotropical paleobotany. IV. The Eocene communities of Panama. Ann. Missouri Bot. Gard. 72: 504–534.

———. 1987. Miocene communities and paleoenvironments of southern Costa Rica. Amer. J. Bot. 74: 1501–1518.

———. 1988a. Studies in neotropical paleobotany. V. The lower Miocene communities of Panama—the Culebra Formation. Ann. Missouri Bot. Gard. 75: 1440 1466.

———. 1988b. Studies in neotropical paleobotany. VI. The lower Miocene communities of Panama the Cucaracha Formation. Ann. Missouri Bot. Gard. 75: 1467–1479.

———. 1989. Studies in neotropical paleobotany. VII. The lower Miocene communities of Panama—the La Boca Formation. Ann. Missouri Bot. Gard. 76: 50–66.

———. 1991a. Studies in neotropical paleobotany. IX. The Pliocene communities of Panama angiosperms (dicots). Ann. Missouri Bot. Gard. 78: 201 223.

———. 1991b. Studies in neotropical paleobotany. X. The Pliocene communities of Panama composition, numerical representations, and paleocommuniity paleoenvironmental reconstructions. Ann. Missouri Bot. Gard. 78: 465–475.

———. 1995. Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. Biotropica 27: 20–27.

———. 1998. Studies in neotropical paleobotany. XI. Late Tertiary vegetation and environments of southeastern Guatemala: palynofloras from the Mio-Pliocene Padre Miguel Group and the Pliocene Herrería Formation. Amer. J. Bot. 85: 1409–1425.

———. 1999a. Late Cretaceous and Cenozoic history of North American vegetation (north of Mexico). Oxford Univ. Press, New York.

———. 1999b. The Tertiary history of the northern temperate element in the northern Latin American biota. Amer. J. Bot. 86: 32–38.

———. 1999c. Studies in neotropical paleobotany. XIII. An Oligo-Miocene palynoflora from Simojovel (Chiapas, Mexico). Amer. J. Bot. 86: 17–31.

———. 2003a. Geohistory models and Cenozoic paleoenvironments of the Caribbean region. Syst. Bot. 28: 378–386.

———. 2003b. The concepts of deep-time floras and paleobotanical hot-spots. Syst. Bot. 28: 461–464.

———. 2003c. Historical phytogeography of the Greater Antilles. Brittonia 55: 357–383.

——— & D. M. Jarzen. 1969. Studies in neotropical paleobotany. I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308–357.

Grimm, E. C., G. L. Jacobson, Jr., W. A. Watts, B. C. S. Hansen & K. A. Maasch. 1993. A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich events. Science 261: 198–200.

Gruas-Cavagnetto, C. 1976. Etude palynologique du Paléogène du sud de l'Angleterre. Cah. Micropaléontol. 1: 1–49.

———. 1991. Pollens de dinophycées de l'Lerdien moyen (Eocène inférieur) de Fordones (Corbières, France). Cah. Micropaléontol., N.S. 6: 51–66.

———, M. Laurain & R. Meyer. 1980. Un sol de mangrove fossilizé dans les lignites du Soissonnais (Yprésien) à Verzenay (Marne). Geobios 16: 795–801.

———, Y. Tambareau & J. Villatte. 1988. Données paléoécologiques nouvelles sur le Thanétien et l'Lerdien de l'avant-pays pyrénéen et de la Montagne Noire. Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry 25: 219–235.

Guilderson, T. P., R. G. Fairbanks & J. L. Rubenstone. 1994. Tropical temperature variations since 20,000 years ago: modulating interhemispheric climatic change. Science 263: 663–665.

Habib, D., D. Thurber, D. Ross & J. Donahue. 1970. Holocene palynology of the Middle American Trench near Tehuantepec, Mexico. Mem. Geol. Soc. Amer. 126: 233–261.

Harland, W. B., R. L. Armstrong, A. V. Cox, L. E. Craig, A. G. Smith & D. G. Smith. 1989. A geologic time scale 1989. Cambridge Univ. Press, Cambridge.

Hekel, H. 1972. Pollen and spore assemblages from Queensland Tertiary sediments. Publ. Geol. Surv. Queensland 355 (Palaeontol. Pap. 30): 1 33.

Hollick, A. 1928. Paleobotany of Porto Rico. New York Academy of Sciences Scientific Survey of Porto Rico and the Virgin Islands 7: 177–393.

Hoorn, C. 1994a. Miocene Palynostratigraphy and Paleoenvironments of Northwestern Amazonia. Evidence for Marine Incursions and the Influence of Andean Tectonics. PhD. Dissertation, Univ. Amsterdam.

———. 1994b. An environmental reconstruction of the palaeo-Amazon River system (middle-late Miocene, NW Amazonia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 112: 187–238.

———. 1994c. Fluvial paleoenvironments in the intracratonic Amazonas Basin (early Miocene-early middle Miocene, Colombia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 1–54.

Horton, B. K., B. A. Hampton & G. L. Waanders. 2001. Paleogene synorogenic sedimentation in the Altiplano Plateau and implications for initial mountain building in the Central Andes. Geol. Soc. Amer. Bull. 113: 1387–1400.

Jarzen, D. M. 1978. Some Maestrichtian palynomorphs and their phytogeographical and paleoecological implications. Palynology 2: 29–38.

Krutzsch, W. 1969. Über einige stratigraphisch wichtige neue longaxoner-Pollen aus dem mittleuropäischen Alttertiär. Geologie 18: 379–510.

———. 1970. Die stratigraphisch verwertbaren Sporen- und Pollenformen des mitteleuropäischen Alttertiärs. Jahrbücher für Geologie 3: 309–379.

——— & R. Vanhoorne. 1977. Die Pollenflora von Epinois und Loksbergen in Belgien. Palaeontographica B 163: 1–110.

Lakhanpal, R. N. 1970. Tertiary floras of India and their bearing on the historical geology of the region. Taxon 19: 675–694.

LaMotte, R. S. 1952. Catalogue of the Cenozoic plants of North America through 1950. Mem. Geol. Soc. Amer. 51: 1–381.

Langenheim, J. H., B. L. Hackner & A. Bartlett. 1967. Mangrove pollen at the depositional site of the Oligo/Miocene amber of Chiapas, Mexico. Bot. Mus. Leafl. 21: 289–324.

Leg 119 Shipboard Scientific Party. 1988. Early glaciation of Antarctica. Nature 333: 303–304.

Leopold, E. B. 1969. Miocene pollen and spore flora of Eniwetok Atoll, Marshall Islands. Profess. Pap. U.S. Geol. Surv. 260-II: 1133–1185.

Leyden, B. A., M. Brenner, D. A. Hodell & J. A. Curtis. 1994. Orbital and internal forcing of climate on the Yucatan Peninsula for the past ca. 36 ka. Palaeogeogr. Palaeoclimatol. Palaeoecol. 109: 193–210.

Lorente, M. A. 1986. Palynology and palynofacies of the upper Tertiary in Venezuela. Diss. Bot. 99. J. Cramer, Berlin.

Machin-Pallot, J. 1971. Plant microfossils from Tertiary deposits of the Isle of Wight. New Phytol. 70: 851–872.

Macphail, M. K. 1999. Palynostratigraphy of the Murray Basin, inland southeastern Australia. Palynology 23: 197–240.

Martínez-Hernández, E. 1992. Caracterización ambiental del Terciario de la region de Ixtapa, estado de Chiapas—un enfoque palinoestratigráfico. Revista Univ. Nac. Autón. México 10: 54–64.

Melchior, H. 1964. Rhizophoraceae. Pp. 357–359 *in* H. Melchior (editor), Engler's Syllabus der Pflanzenfamilien, 12th ed., vol. 2. Gerbrüder Bornträger, Berlin, Germany.

Mepham, R. H. 1983. Mangrove floras of the southern continents, part 1: the geographical origin of Indo-Pacific mangrove genera and the development and present status of the Australian mangroves. S. African J. Bot. 2: 1–8.

Miller, K. G., R. G. Fairbanks & G. S. Mountain. 1987. Tertiary oxygen isotope synthesis, sea level history, and continental margin erosion. Paleoceanography 2: 1–19.

Moncada Ferrera, M., C. E. Hernández Fuentes & M. Cabrera Castellanos. 1990–1991. Anális polínico de sedimentos marinos del occidente de la Isla de la Juventud (Cuba). Acta Bot. Hung. 36: 145–161.

Morley, R. J. 1977. Palynology of Tertiary and Quaternary sediments in southeast Asia. Proceeding of the Indonesian Petroleum Association, 6th Annual Convention: 255–276.

———. 2000. Origin and Evolution of Tropical Rain Forests. John Wiley & Sons, New York.

Muller, J. 1964. A palynological contribution to the history of the mangrove vegetation in Borneo. Pp. 33–42 *in* L. M. Cranwell. Ancient Pacific Floras. Univ. Hawaii Press, Honolulu.

———. 1981. Fossil pollen records of extant angiosperms. Bot. Rev. 47: 1–142.

——— & C. Caratini. 1977. Pollen of *Rhizophora* (Rhizophoraceae) as a guide fossil. Pollen & Spores 19: 361–389.

Pares Regali, M. S., N. Uesugui & A. S. Santos. 1974a. Palinología dos sedimentos meso-Cenozoicas do Brasil (I). Bol. Técn. Petrobras (Rio de Janeiro) 17: 177–191.

——, ——— & ———. 1974b. Palinología dos sedimentos meso-Cenozoicas do Brasil (II). Bol. Técn. Petrobras (Rio de Janeiro) 17: 263–301.

Petriella, B. 1972. Estudio de maderas petrificadas del Tertiario inferior del area central de Chubut (Cerro Bororo). Revista Mus. La Plata 6: 159–254.

Plaziat, J.-C., C. Cavagnetto, J.-C. Koeniguer & F. Blatzer. 2001. History and biogeography of the mangrove ecosystem, based on a critical reassessment of the paleontological record. Wetlands Ecol. Managem. 9: 161–179. [Special issue: Life on the Edge: Past and Future of Mangroves, N. C. Duke & A. E. Schwarzbach, editors.]

Poore, R. Z. & R. K. Matthews. 1984. Oxygen isotope ranking of late Eocene and Oligocene planktonic foraminifera: implications for Oligocene sea-surface temperatures and global ice-volume. Mar. Micropaleontol. 9: 111–134.

Prakash, U. 1960. A survey of the Deccan Intertrappean flora of India. J. Paleontol. 34: 1027–1040.

Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

Rico-Gray, V. 1993. Origen y rutas de dispersión de los mangles: una revisión con énfasis en las especies de América. Acta Bot. Mex. 25: 1–13.

Rull, V. 1998. Middle Eocene mangroves and vegetation changes in the Maracaico Basin, Venezuela. Palaios 13: 287–296.

Saenger, P. 1998. Mangrove vegetation: an evolutionary perspective. Austral. J. Mar. Freshwater Res. 49: 277–286.

Schwarzbach, A. E. & R. E. Ricklefs. 2000. Systematic affinities of Rhizophoraceae and Anisophylleaceae, and intergeneric relationships within Rhizophoraceae, based on chloroplast DNA, nuclear ribosomal DNA, and morphology. Amer. J. Bot. 87: 547–564.

—— & ———. 2001. The use of molecular data in mangrove plant research. Wetlands Ecol. Managem. 9: 195–201. [Special issue: Life on the Edge: Past and Future of Mangroves, N. C. Duke & A. E. Schwarzbach, editors.]

Shackleton, N. J. & N. D. Opdyke. 1977. Oxygen isotope and paleomagnetic evidence for early northern hemisphere glaciation. Nature 270: 216–219.

Thanikaimoni, G. 1987. Mangrove palynology. Trav. Sect. Sci. Techn. Inst. Franç. Pondichéry 24: 1–100.

Tomasini-Ortiz, A. C. & E. Martínez-Hernández. 1984. Palinología del Eocene-Oligoceno de Simojovel, Chiapas. Paleontol. Mex. 50: 1–49.

van der Hammen, T. & T. A. Wijmstra. 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. Leidse Geol. Meded. 30: 183–241.

Velenovský, J. & L. Viniklář. 1926. Flora Cretacea Bohemiae. Czechoslovakia Statního Geologického Ústavu Rozpravy pt. 2: 1–51, 8–17.

Venkatachala, B. S. & M. S. Rawat. 1972. Palynology of the Tertiary sediments in the Cauvery Basin. I. Palaeocene-Eocene palynoflora from the subsurface. Pp. 292–335 *in* A. K. Ghosh, Seminar in Paleopalynology and Indian Stratigraphy. A. K. Ghosh, Calcutta.

——— & ———. 1973. Palynological zonation of the Tertiary sub-crop sequence in the Cauvery Basin, south India. Proceedings of the III International Palynology Conference, Palynology of the Cenophyte: 73–78.

Wijmstra, T. A. 1971. The palynology of the Guiana coastal basin. Drukkerij de Kempenaeo, Oegstgeest.

Wilkinson, H. P. 1983. Starch grain casts and moulds in Eocene (Tertiary) fossil mangrove hypocotyls. Ann. Bot. 51: 39–45.

Wolfe, J. A. 1972. An interpretation of Alaskan Tertiary floras. Pp. 201–233 *in* A. Graham. Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Science Publishers, Amsterdam.

———. 1977. Paleogene floras from the Gulf of Alaska region. Profess. Pap. U.S. Geol. Surv. 997: 1–108.